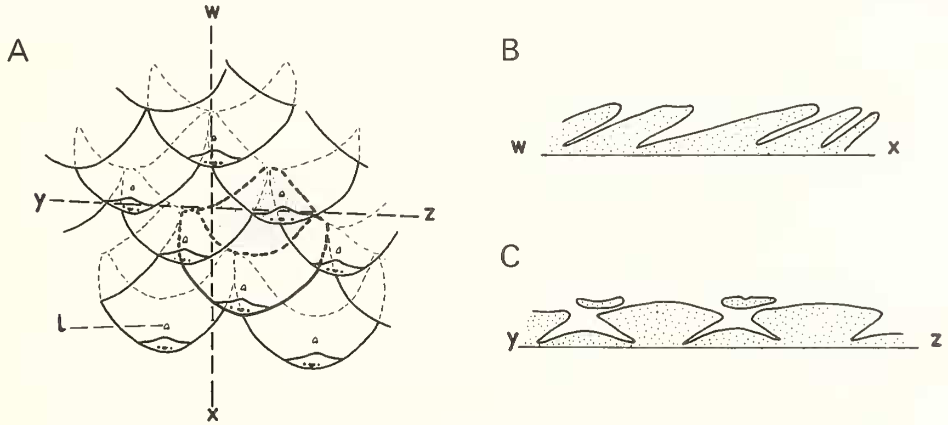
EPIDERMAL STUDIES IN THE INTERPRETATION OF *LEPIDOPHLOIOS* SPECIES

by B. A. THOMAS

ABSTRACT. Epidermal details are described from the leaf cushions of five species of *Lepidophloios* including one new species *L. grangeri*. Such epidermal information allows the species to be distinguished more accurately. Cushion variation within a species is also considered, with epidermal studies verifying the conspecificity of specimens. It is suggested that young *Lepidophloios* cushions are of the *Lepidodendron* form, which subsequently enlarged to increase their photosynthetic ability.

LEPIDOPHLOIOS is a genus of arborescent lycopod stems very similar to *Lepidodendron* in size, general morphology, and in having a dense covering of spirally arranged leaves. All but the terminal shoots of both genera shed the apical parts of their leaves, retaining only their basal portions as the familiar leaf cushions. The main distinguishing feature is that in *Lepidophloios* most cushions characteristically bulge outwards and downwards in such a manner that they overlap each other and show rounded lateral and basal angles (text-fig. 1). The leaf scars appear at the bases of the visible portions of the leaf cushions and are always broader than long, usually with one vascular print and two parichnos scars. Therefore the only part of the cushion normally visible is the upper half representing the basal portion of the adaxial leaf surface. The lower half, or abaxial surface, is hidden.

Confusion has, however, existed about the separation of these two genera and opinions have varied about the determinations of some specimens. This problem



TEXT-FIG. 1. Drawings to illustrate the main feature of the *Lepidophloios* leaf cushion. A, leaf cushions, l—ligule pit aperture. The stippled area of the heavy print cushion represents the area of connection of the cushion to the stem. B and C, diagrammatic sections through uncompressed leaf cushions. The lines of section are shown on fig. A.

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is accentuated when specimens are mistakenly inverted. For example, specimens of *L. acerosus* Lindley and Hutton have been mistaken for species of *Lepidodendron* and figured inverted, while specimens of *Lepidodendron* have been figured upside-down and described as species of *Lepidophloios*. Such determinations have naturally proved troublesome in the literature and the more important are returned to later.

Confusion of this kind is best avoided by careful study and recognition of the finer cushion details. General shape with suggestions of cushion overlap is insufficient for generic determination as a few species of *Lepidodendron* show this feature in their upper angles (e.g. *L. mannabachense* Presl., Thomas 1970, pl. 32, figs. 3, 4, 6, 7). One such specimen from the Black Bed Coal of Yorkshire clearly illustrates such a possible confusion. Both Kidston (1893, p. 555, pl. 1, fig. 4) and Crookall (1964, p. 307, pl. 75, fig. 6) described it as *Lepidophloios laricinus* but I believe it to be *Lepidodendron mannabachense*. I have therefore figured some of its leaf cushions correctly and inverted to show how one can be misled by incorrect orientation (Pl. 33, figs. 1, 2). Such cushions presumably bulged outwards more above than below the leaf scars which could then have given this marginal overlap during compression. It is far safer to look for the ligule pit apertures, the parichnos, and the foliar prints, as their positioning is only slightly variable. The ligule pit is always above the leaf scar; the parichnos, when present, are invariably below the leaf scar; while the three foliar prints normally form an arc in the lower half of the leaf scar with the vascular print being slightly below the level of the other two. Even surface ornamentation can sometimes be a valuable guide as certain *Lepidodendron* species have their cushions distinctly striated above the leaf scar which is a feature not shown by *Lepidophloios*.

The cushion cuticles are described here in some detail for the first time, although certain structural details of their guard cells have already been discussed (Thomas 1974). All show the same general arrangements of epidermal cells and stomata as those described from *Lepidodendron* (Thomas 1970). Cuticle was prepared by macerating portions of compression in Schulze solution (concentrated nitric acid and about 5% potassium chlorate) normally followed by clearing in dilute ammonia solution. Some cuticles were mounted unstained in glycerine jelly and examined by normal transmitted light, supplemented in some instances by phase-contrast illumination. These prepared slides have been deposited with their respective specimens. Other cuticles were coated with gold/palladium and studied with a 'Stereoscan' Scanning Electron Microscope. A range of specimens was examined for most species in an attempt to detect any variation, but this was often prevented by a lack of suitable material. Many specimens are preserved as impressions from which all the compression has either disappeared during fossilization or has been removed since collection. Even when some compression remains it is often badly cracked so that it does not yield cuticle in usable-sized fragments.

The most important specimens examined are listed for each species discussed. They belong to, or were deposited in, the British Museum of Natural History, London (BMNH); the Czechoslovakian National Museum, Prague (CNM); the Institute of Geological Sciences: Kidston Collection, London (K) and the general collections of London (IGSLond), Leeds (IGSLds), and Edinburgh (IGSE).

SYSTEMATIC DESCRIPTIONS

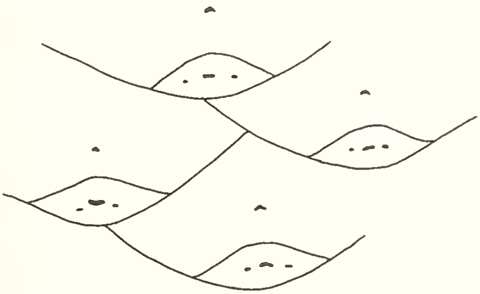
Lepidophloios laricinus Sternberg

Plate 33, figs. 1–6; Plate 34, figs. 1–3; text-figs. 2, 3

1820 *Lepidodendron laricinum* Sternberg, p. 21, pl. 11, figs. 2–4.
1875 *Lepidophloios laricinum* Sternberg; Feistmantel, p. 191, pl. 33, figs. 1–4; pl. 34, figs. 1–4.
1904 *Lepidophloios laricinus* Sternberg; Zalessky, pp. 30, 99, pl. 6, figs. 8, 10; pl. 7, figs. 1, 2; pl. 8, figs. 7, 9.
1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 307, pl. 74, fig. 5; text-figs. 98, 100*c*.

Material. Type specimen, CNM ČGH316, from the Wranowitzer Shaft in the Radnice Coalfield, Central Bohemia (uppermost Westphalian B–C); BMNH V58739 from Kamenný Újezd, near Nýřany, Plzen district, West Bohemia (Upper Westphalian B–D?); IGSLds V4486b from above the Main Seam, Newbiggin Colliery, Northumberland—Westphalian B; IGSLond 15027 from Dysart, near Kirkaldy, Fife—Westphalian A or B.

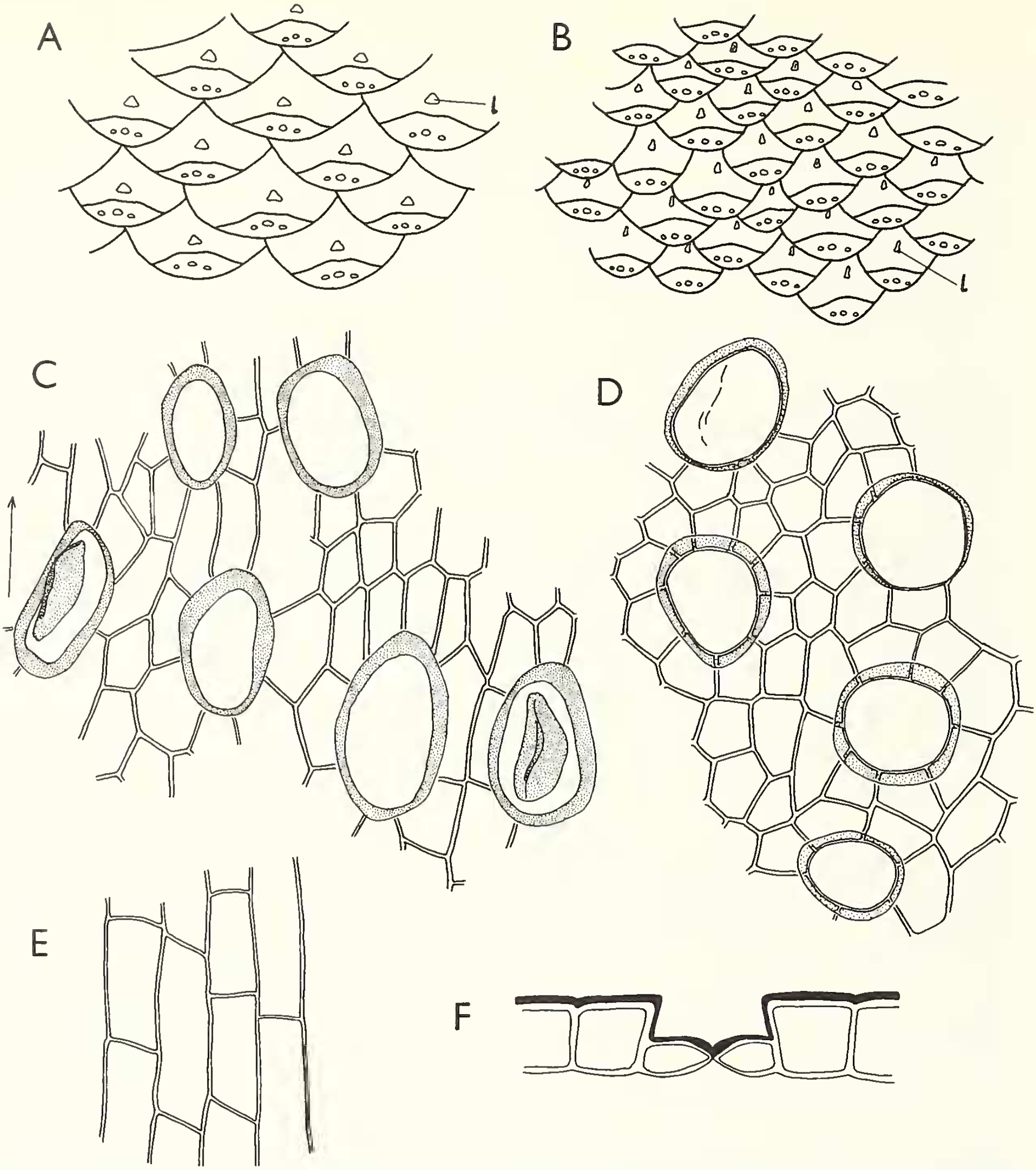
All the specimens accepted here are of the same general cushion morphology in having downward bulging and overlapping leaf cushions. They all appear to be from mature stems, mostly of large diameters, and none are known which might be thought to come from terminal shoots still retaining the distal lamina portions of their leaves. Visible portions of the overlapping cushions are normally much broader than long although in a few specimens these dimensions are nearly equal. Distinct keels are never present on the cushions but sometimes their surfaces bulge in the median line giving the appearance of a very indefinite keel. The three foliar prints are usually in the lower half of the leaf scar but occasionally they can be found in the upper half. The type specimen was figured by Sternberg without ligule pit apertures on the leaf cushions, but re-examination shows indistinct pit scars about 1·5 mm above the leaf scars (text-fig. 2). This species has often been quoted as having its ligule pit scars a little distance above the leaf scars and in general comparison with other species this appears to be correct. Crookall (1964) cites K 6142, from Glenburn and Hilton Colliery, Skelmersdale, Lancashire, as an exception to this. However, as the visible cushion areas are only 2·0 mm long and 3·5 mm broad, one can hardly expect there to be a very large distance between these two scars. Cushion size will naturally determine the length or area of certain individual features and no definite sizes or areas should ever be quoted.



TEXT-FIG. 2. *Lepidophloios laricinus* Sternberg. Type specimen CNM ČGH316, × 2.

The type specimen is an impression and unfortunately the very little remaining compression gave no cuticle. Preparations were, however, made from BMNH V58739, which came from the same area as the type, and from IGSLds V4486b and IGSLond 5027.

Cuticle description. The epidermal cellular arrangement appears to be virtually identical on both the exposed and hidden leaf cushion surfaces. Most of the cells

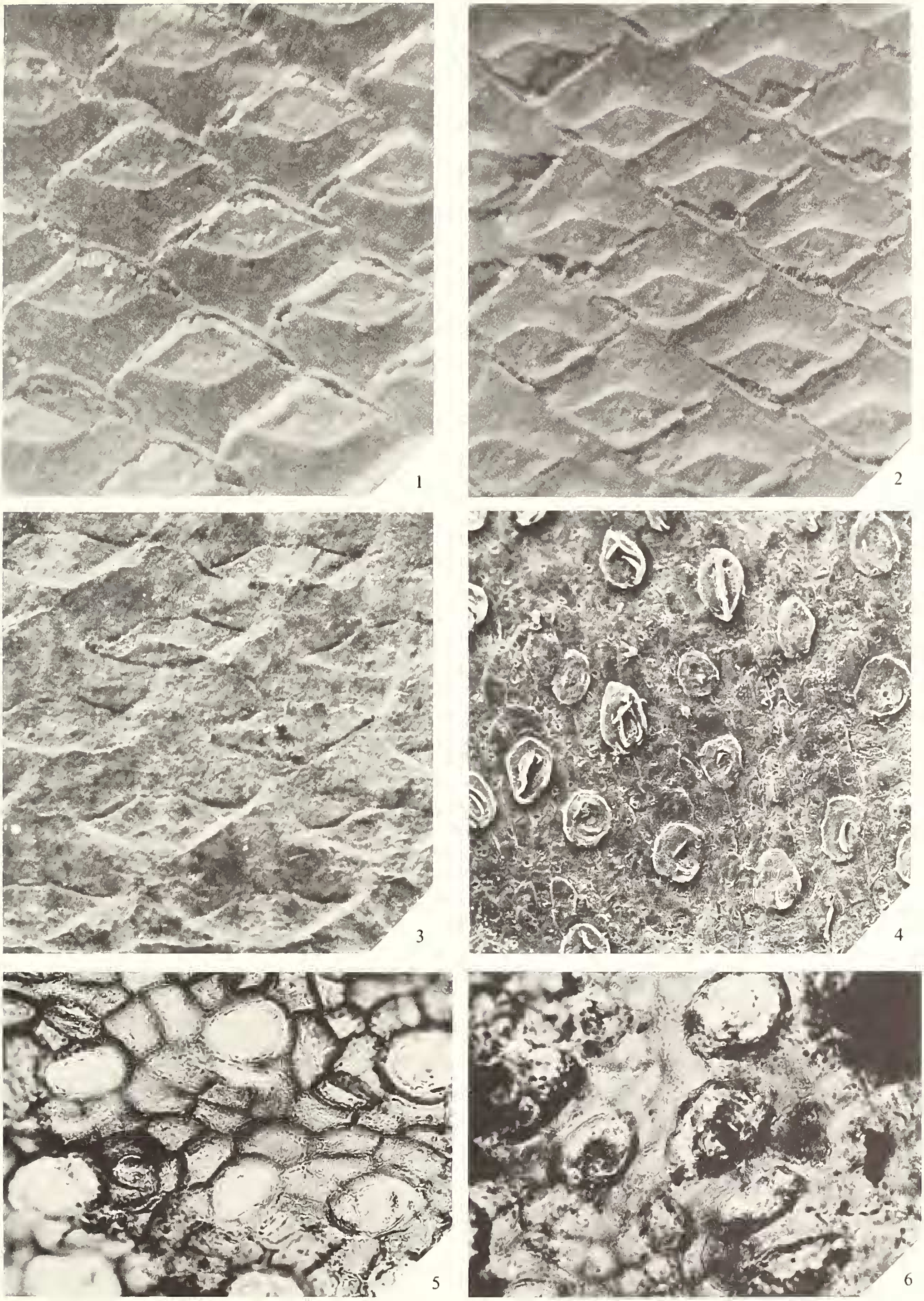


TEXT-FIG. 3. *Lepidophloios laricinus* Sternberg. A, BMNH V4486b, ×2. B, IGSLond 15027, ×2, l—ligule pit aperture. C–F, cuticle from BMNH V58739. C, cuticle from median area of the cushion, ×400; drawn from the undersurface; slide no. V58739a. Arrow directed parallel to the vertical axis of the cushion. D, cuticle from the non-median area of the cushion, ×400; drawn from the undersurface; slide no. V58739b. E, ligule pit cuticle, ×400; slide no. V58739c. F, diagrammatic median transverse section of a stoma, ×500.

EXPLANATION OF PLATE 33

Figs. 1 and 2. *Lepidodendron mannabachense* Presl. K 1404 from above the Black Bed Coal, Low Moor, Yorkshire; both illuminated from the top left, ×3. 1, orientated correctly. 2, inverted showing '*Lepidophloios*' characters.

Figs. 3–6. *Lepidophloios laricinus* Sternberg. IGSLds V4466B from above the Main Seam, Newbiggin Colliery, Northumberland, ×4. 4–6, cuticle prepared from BMNH V58739; 4, SEM., ×200; 5, 6, transmitted light photographs; slide no. V58739a, ×350.



THOMAS, *Lepidophloios*

are elongated along the length of the cushion and about 40 μm $\times$ 15 μm in size, although those near the cushion sides are isodiametric and about 15 μm large. Their anticlinal walls are straight, smooth, and 2 μm thick, while the periclinal walls are flat and smooth. Stomata are randomly arranged on the cushion at about 250 per mm^2 and orientated roughly parallel to the vertical axis of the cushion. Individual stomata have an average size of 45 μm $\times$ 30 μm, having an observed range of about 40–60 μm $\times$ 23–40 μm, with guard cells sunken in pits about 6–10 μm deep. The ligule pit cuticles are about 0·7 mm broad, but no length measurements were possible due to their fragmentation during preparation. The pit wall cells are rectangular, 50 μm $\times$ 16 μm large, longitudinally elongated, and in vertical rows. The anticlinal walls are straight, smooth, and about 2 μm thick; the periclinal walls are flat and smooth.

Comparison. L. laricinus has been described from both the Upper and the Lower Carboniferous rocks of Great Britain, but it is here restricted to the Upper Carboniferous with a reassignment of the Lower Carboniferous specimens. K 1828, from the Carboniferous Limestone Series of Grange, Linlithgowshire in Scotland, was originally described by Kidston (1893*b*, p. 560) as *L. macrolepidotus* and by Crookall (1964) as *L. laricinus*. Here I am redescribing it as *L. grangeri* sp. nov. (p. 286). IGSE 1296, described by Crookall (1939, p. 14, pl. 2, fig. 2) from the Scottish 'Millstone Grit' at Cambus, near Alloa, Clackmannanshire, has already been referred to *Lepidodendron rhodianum* Sternberg (Thomas 1970, p. 168, text-fig. 12). The specimens of *Lepidophloios laricinus* described by Crookall (1964, p. 310) from the Carboniferous Limestone Series of Scotland differ in two aspects of cushion morphology. They have more prominently raised median areas to their cushions and have ligule pit apertures adjacent to the upper edges of the leaf scars. No cuticles could be prepared, but the differences in cushion morphology seem sufficient to strongly question their inclusion within this species and it seems more prudent to keep them separate. They are equally unlike all the other described species, but it is not intended at present to give them a new name. This view is then in agreement with that of Kidston who had originally labelled these specimens as *Lepidophloios* sp.

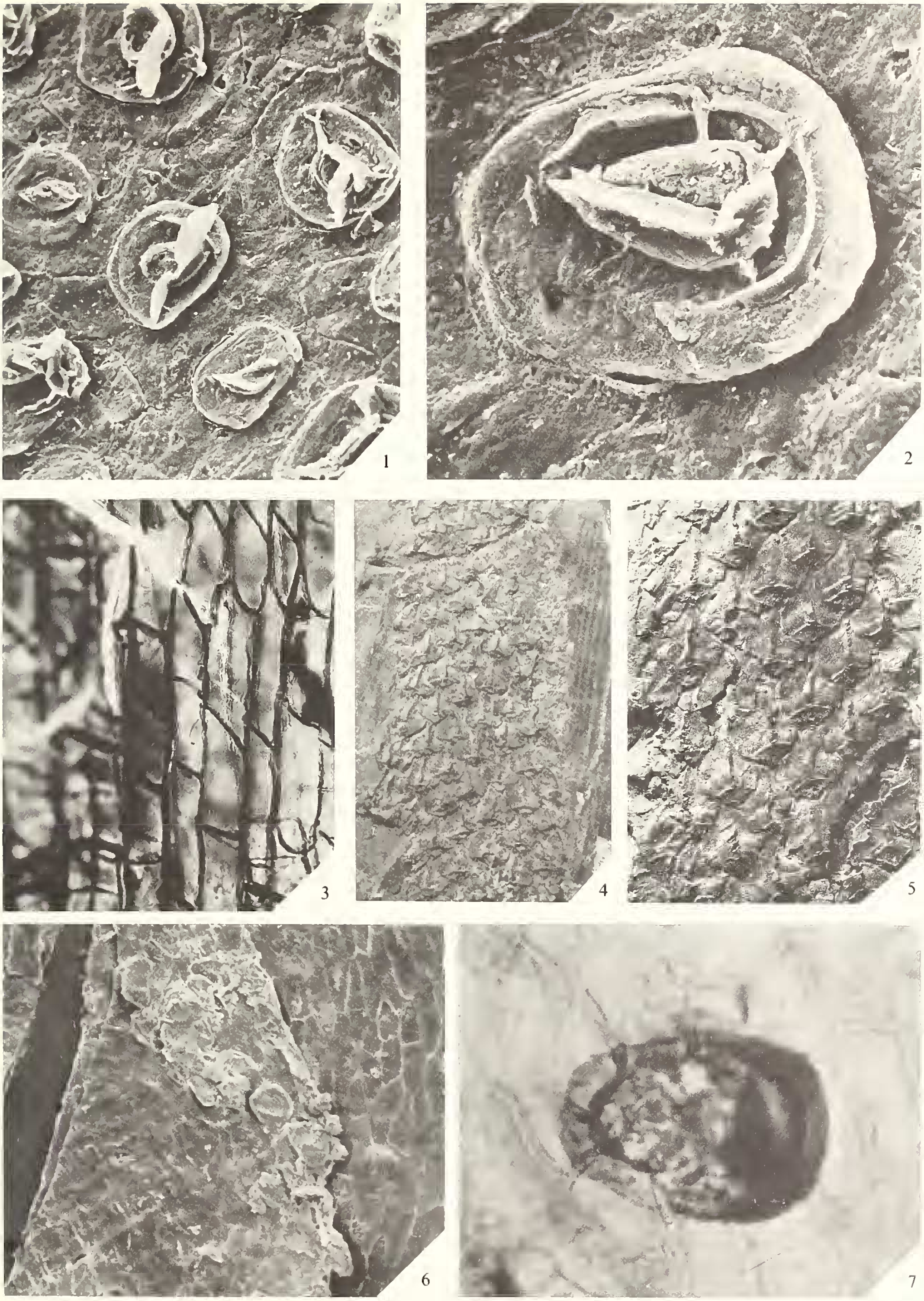
Those specimens (K 4991–4992) quoted by Crookall (1964, p. 312, pl. 74, figs. 3, 4) as examples of small shoots showing upturned and undeflected leaf cushions are also excluded here from this species. They are instead reassigned to Kidston's original determination of *L. acerosus* on the basis of both cushion morphology and epidermal characters seen in cuticle preparations.

EXPLANATION OF PLATE 34

Figs. 1–3. *Lepidophloios laricinus* Sternberg. Cuticles prepared from BMNH V58739. 1, cushion cuticle; SEM., $\times$500. 2, stoma; SEM., $\times$1500. 3, ligule pit cuticle; slide no. V58739c, $\times$350.

Figs. 4–7. *Lepidophloios acerosus* Lindley and Hutton. 4, K 4947 from above the Parkgate Coal (Old Hards), Hartley Bank Colliery, Horbury, Yorkshire, $\times$1. 5, K 764 from above the Kiltongue Coal, Foxley, near Glasgow, $\times$2. 6, SEM. showing cushion cuticle from above and below the leaf scar of K 764, $\times$200. 7, stoma photographed with transmitted light; slide no. PF 3195, $\times$1200.

PLATE 34



THOMAS, *Lepidophloios*

Lepidophloios acerosus Lindley and Hutton

Plate 34, figs. 4–7; Plate 35, figs. 1, 2; text-fig. 4

1831 *Lepidodendron acerosum* Lindley and Hutton, pl. 7, fig. 1; pl. 8.
1837 *Lepidostrobus pinaster* Lindley and Hutton, pl. 198.
1893*b* *Lepidophloios acerosus* Lindley and Hutton; Kidston, p. 558, pl. 1, fig. 1; pl. 2, fig. 9.
1901 *Lepidophloios acerosus* Lindley and Hutton; Kidston, p. 54, text-fig. 7*c* (inverted).
1914 *Lepidophloios acerosus* Lindley and Hutton; Arber, pp. 396, 415, 444, pl. 28, fig. 20 (inverted).
1917 *Lepidophloios acerosus* Lindley and Hutton; Kidston, pp. 1057, 1080, 1083, pl. 2, fig. 5 (inverted).
1929 *Lepidophloios acerosus* Lindley and Hutton; Crookall, p. 26, pl. 3, fig. 50; pl. 22, fig. k (both inverted).
1974 *Lepidophloios acerosus* Lindley and Hutton; Crookall, p. 313, pl. 75, fig. 7; pl. 76, fig. 2; pl. 79, fig. 5 (inverted); text-fig. 100*d*.

Material. K 764 from above the Kiltongue Coal, Foxley, near Glasgow, Lanarkshire—communis Zone, Westphalian A; K 3459 from above the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire—communis Zone, Westphalian A; IGSLds RC 1778 from above the Ince Yard Mine, Mains Colliery, near Wigan, Lancashire—modiolaris Zone, Westphalian A; K 4991 and BMNH V33591 from above the Barnsley Red, Monkton Main Colliery, near Barnsley, Yorkshire—similis pulchra Zone, Westphalian B; IGSLond KP 449 from above the No. 5 seam Chislet Colliery, Kent—Transition Coal Measures, Westphalian ?C; K 6284 from above the Hafod Rider Seam, Hill's Plymouth Colliery, Pentrebach, near Merthyr, Glamorgan—upper similis pulchra Zone, Westphalian B; K 6142 from Glenburn and Hilton Colliery, 1 mile NE. of Skelmersdale, Lancashire—Westphalian?; K 3634, from above the Fulledge or Yard Mine, New Shaft, Bank Hall Colliery, Burnley, Lancashire—Westphalian B; K 4992 from above the Pargate Coal, Church Lane Colliery, Dodworth, near Barnsley, Yorkshire—modiolaris Zone, Westphalian A.

The widely recognized and described form of *L. acerosus* is a typical '*Lepidophloios*' stem with downturned and overlapping leaf cushions. The exposed cushion areas are longer than broad but their relative dimensions vary slightly with size and the amount of interdependent overlap. Definite cushion keels are usually present but in some specimens they are only slightly raised. The three foliar prints are usually in the lower halves of the leaf scars although they are sometimes nearly central. Ligule pit apertures occur just above the leaf scars, although as Crookall (1964, p. 312) has shown they can be sometimes slightly separated.

The smallest shoots are rather different in having undeflected smaller leaf cushions which could be referred to the genus *Lepidodendron*. Specimens K 3634, K 4991–4992, K 6142, and K 6284 possess cushions of this kind, while BMNH V33591 also possesses more 'normal' slightly elongated and downward defected, leaf cushions as its lower end. Kidston (1893*b*, pl. 1, fig. 1) described a small leafy shoot with upturned leaf cushions as *Lepidophloios acerosus*, but I would agree with Jongmans

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EXPLANATION OF PLATE 35

Figs. 1, 2. *Lepidophloios acerosus* Lindley and Hutton. Cuticle from the cushion surface above the leaf scar of K 764. 1, SEM. photograph showing stomata and epidermal cells, ×500. 2, cushion cuticle with ligule pit cuticle; slide no. PF 3196, ×125.

Figs. 3–6. *Lepidophloios macrolepidotus* Goldenberg, from the roof of the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire. 3, K 3256, ×3. 4, K 3257, ×3. 5, 6, cuticle from K 3256; slide no. PF 2895. 5, ×250; 6, ×550.

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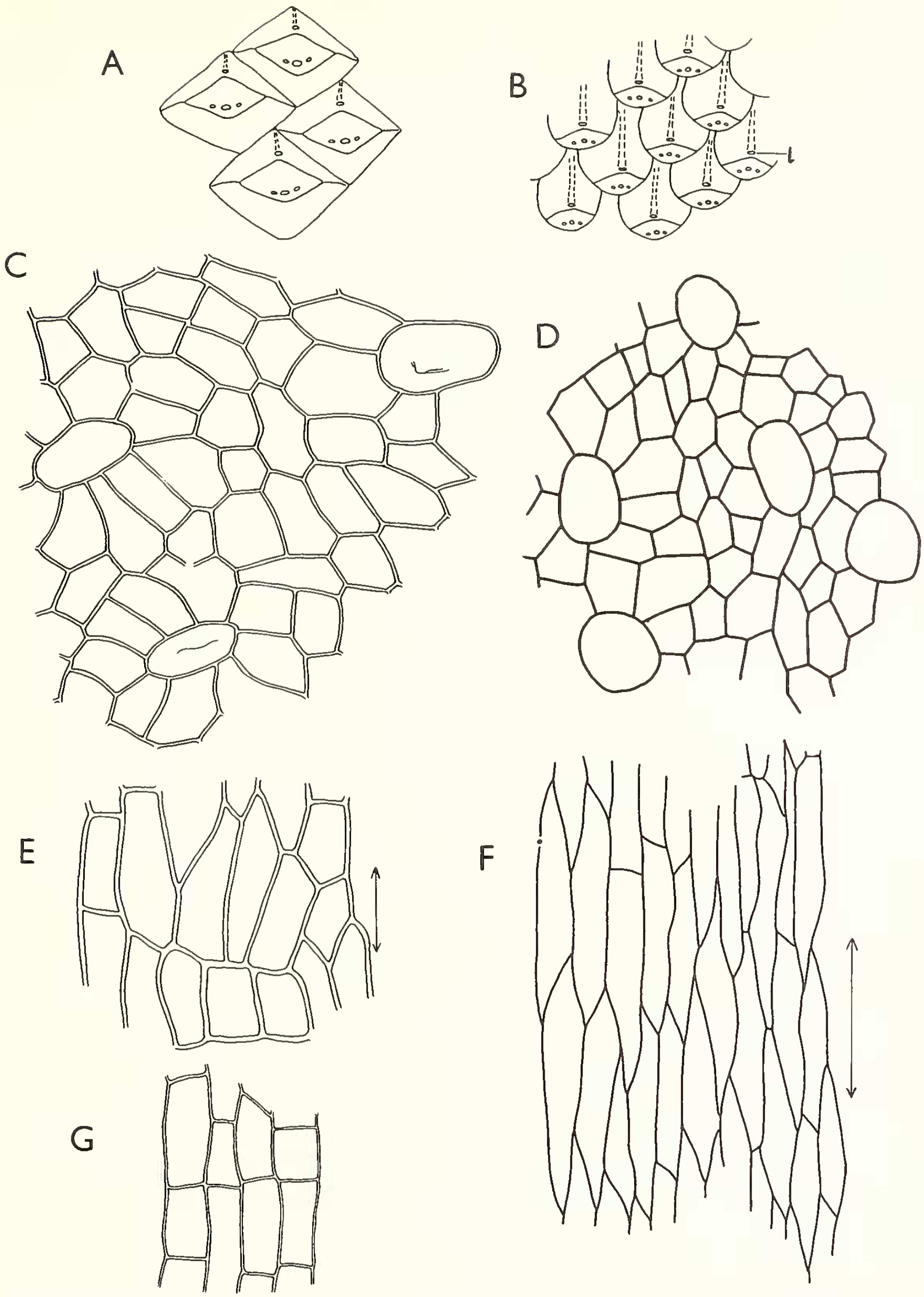
(1930, p. 40) and Crookall (1964, p. 315) that, on the basis of the visible cushion morphology, there appears to be no good reason for including it within this species.

A comparison of these stems reveals several interesting facts which are relevant to a consideration of their growth patterns. The undeflected cushions of K 4991 and K 4992 are about 5·0 mm long and 5·5 mm broad, therefore being larger than the smallest of the 'more usual' deflected cushions of IGSLond 3459. The cushions on K 764 and K 4947 show a progressive increase in size down the stem, while the former also exhibits a corresponding increase in shoot diameter. There are therefore shoots with either non-deflected or deflected leaf cushions suggesting that this may be an expression of subsequent growth of the cushions; an idea supported by those specimens showing a gradual basipetal increase in cushion size. This is clearly a complex subject which is not yet fully understood but we shall return to it in the general discussion.

Cuticle description. Preparations have been made from a selection of specimens with undeflected and deflected cushions and from cushions of varying sizes. Certain general characteristics can be given for the species although certain slight variations have been noticed. The epidermis is different on the two cushion surfaces (Pl. 34, fig. 6). The epidermal cells from the exposed adaxial surface are isodiametric and about 15–20 μm large over most of the central area, but near the sides they are roughly 30 $\mu m \times 15$ μm and elongated towards the cushion margin. The cells from the hidden abaxial surface are about 60 $\mu m \times 10$ μm large and elongated along the cushion length. Small fragments of cuticle with cells about 50 $\mu m \times 15$ μm large were obtained from some of the larger specimens and although their exact origin is unknown it is suggested that they may have come from the intercushion connecting areas of the stem surface. All the cells have straight, smooth anticlinal walls and flat, smooth periclinal walls. Stomata are present almost solely on the exposed cushion surface (about 180 per mm^2) although a few have been noted on the hidden surface —near the edges where the cells are also not quite so elongated. The average stomatal size is about 35 $\mu m \times 26$ μm with their guard cells superficial or only very slightly sunken. Details of guard cell anatomy have already been given (Thomas 1974, p. 530) and I can add no more to this at present. The ligule pit cuticles have rectangular cells, 25–30 $\mu m \times 10$ μm large, arranged in vertical rows, with straight, smooth anticlinal walls and flat, smooth periclinal walls.

Comparison. The leaf cushions of *L. acerosus* and *L. laricinus* can be distinguished by a number of characters. The cushions of *L. acerosus* are relatively longer and possess definite keels which are never present in the other species. Ligule pit positions are also important as they are normally immediately above and adjacent to the leaf scars in *L. acerosus* but a short distance above them in *L. laricinus*. The cuticle preparations support the distinction between the two species as the epidermal arrangement is different above and below the leaf scars in *L. acerosus* but in *L. laricinus* there is no such distinction. Also the guard cells are sunken in deep pits in *L. laricinus* while they are superficial or only very slightly sunken in *L. acerosus*.

Various emphases have been previously laid on these various morphological characters in an attempt to separate the two species, although no attempts have been made to utilize epidermal characters. Renier (M. S. in Crookall 1964, p. 312)



TEXT-FIG. 4. *Lepidophloios acerosus* Lindley and Hutton. A, BMNH V33591 showing undeflected leaf cushions, ×3. B, IGSLds RC 1778 showing deflected leaf cushions, ×3. C, cushion cuticle from above the leaf scar of V33591, ×400; slide no. V33591a. D–G, cuticle from RC 1778, ×400. D, cushion cuticle from below leaf scar; slide no. PL 279. E, cuticle from cushion edge; slide no. PL 282. F, cushion cuticle from below leaf scar; slide no. PL 279. Arrows directed parallel to the vertical axis of the cushion. G, ligule pit cuticle; slide no. PL 280.

believed the positioning of the ligule pits to be the most important feature while Němejc (1947, p. 78) stressed the relative lengths of the cushions and the presence or absence of keels. In contrast to these, Jongmans (1930) suggested that *L. acerosus* might represent young stems of *L. laricinus* and Stockmans and Willière (1953) similarly believed them to be conspecific. The two species are distinct, but it is certainly better to use more than one cushion character for differentiation, for, as Němejc (1947) and Crookall (1964) have already shown, individual characters are neither always well marked nor constant. The wide range of cushion characters quoted by Crookall is, however, unacceptable and I have here included many of his examples as other species.

L. acerosus has been confused with other species, a problem which has been accentuated by misinterpretation of cushion orientation. Specimens have been figured inverted, as indeed have been specimens of *L. laricinus*. *L. acerosus*, if figured upside-down (e.g. Arber 1914, pl. 28, fig. 20; Kidston 1917, pl. 2, fig. 5; Crookall 1929, pl. 22, fig. k; 1964, pl. 79, fig. 5), could be mistaken for a species of *Lepidodendron*. This could then account for Němejc's (1934) view that there was no difference between *Lepidodendron dichotomum* Sternberg and the figures published for *Lepidophloios acerosus* by West European authors. He thus believed the two species to be closely allied, if not identical, although he did later revert to giving them as distinct species (Němejc, 1946, 1947). A similar confusion seems to have arisen when Weiss (1871) joined *Lepidodendron brevifolium* Ettinghausen (1854) with parts of the *Lepidophloios laricinus* of Goldenberg (1862) and Schimper (1870) under his new name *L. carinatus*. Kidston (1886) then referred *L. acerosus* and *Lepidostrobus pinaster* Lindley and Hutton to *Lepidophloios carinatus* Weiss although he later included all in his synonymy for *L. acerosus* (Kidston 1893*b*, 1894). *L. pinaster* seems to be correctly reidentified as *L. acerosus* but mistakenly believed to be inverted. Jongmans (1929) and Crookall (1964) also appear correct in maintaining that *L. brevifolium* is a species of *Lepidodendron* and that it should therefore be excluded from *Lepidophloios acerosus*.

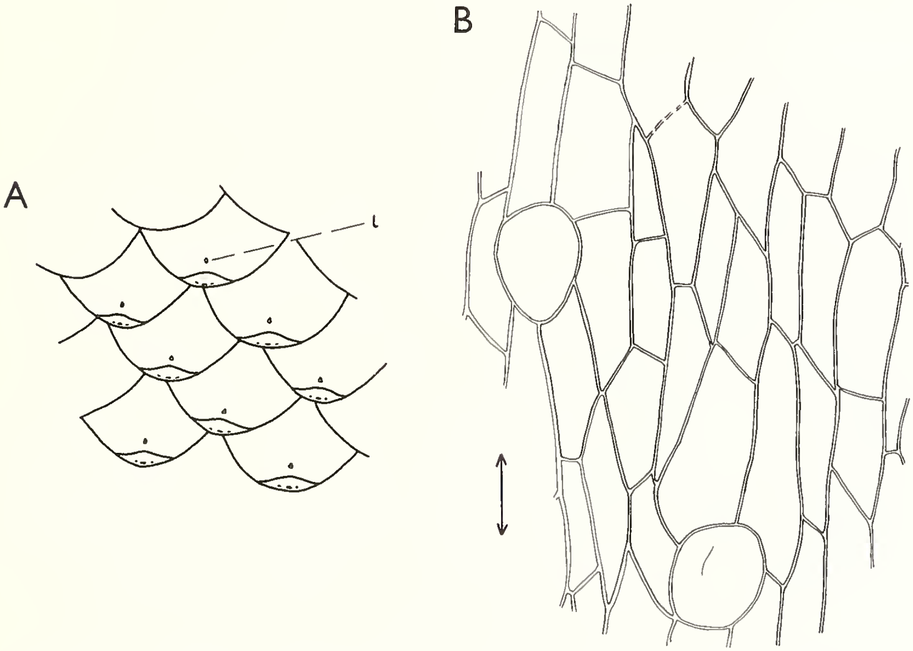
Lepidophloios macrolepidotus Goldenberg

Plate 35, figs. 3–6; text-fig. 5

1855 *Lomatophloyos macrolepidotum* Goldenberg, p. 22.
1862 *Lepidophloios macrolepidotum* Goldenberg, p. 37, pl. 14, fig. 25 (inverted).
1870 *Lepidophloios macrolepidotus* Goldenberg; Schimper, p. 52.
1882 *Lepidophloios macrolepidotus* Goldenberg; Renault, pars, p. 45, fig. 2 (inverted) not fig. 4.
1890 *Lepidophloios macrolepidotus* Goldenberg; Seward, pl. 3, figs. 1–4.
1899 *Lepidophloios macrolepidotus* Goldenberg; Potonié, p. 235, fig. 223.
1959 *Lepidophloios macrolepidotus* Goldenberg; Remy, p. 83, fig. 81.
1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 307, pl. 78, fig. 1 (inverted).
1967 *Lepidophloios macrolepidotus* Goldenberg; Chaloner, p. 571, fig. 390.

Material. K 3256–3257, and IGSLond RC 2910 from above the Fenton Coal, Dodworth Colliery, near Barnsley, Yorkshire—communis Zone, Westphalian A; K4392 from above the Halifax Hard Bed, Fieldhouse Colliery, Deighton, Yorkshire—lenisulcata Zone, Westphalian A.

The largest slab of bark was K 3257, being 180 mm broad, which also had the largest leaf cushions of average visible length 16 mm and breadth 25 mm. All the specimens, however, have leaf cushions of roughly comparable size and shape, being all broader than long with flattened surfaces possessing no keels. The leaf scars have three obvious prints in their lower halves, while the conspicuous ligule pit apertures are triangular in outline and are clearly separated from the leaf scars. The specimens also show a few cushions which appear to be separated from each other, but this is really an illusion caused by narrow strips of adhering shale which can be removed showing the cushions to be continuous and overlapping in the normal manner. Goldenberg (1862) and Renault (1882) figured similar specimens



TEXT-FIG. 5. *Lepidophloios macrolepidotus* Goldenberg. K 3256. A, leaf cushions, ×1, l—ligule pit aperture. B, cushion cuticle, ×400. Arrows directed parallel to the vertical axis of the cushion; slide no. PF 2897.

with cushions separated by bands of what appear to be bark, but these could again be only overlying strips of rock matrix.

Cuticle was prepared from K 3256–3257, and IGSLond RC 2910 but as K 4392 has but a single leaf cushion it was thought unwise to remove any of its compression.

Cuticle description. The epidermis is the same on the exposed and hidden cushion surfaces. Epidermal cells are longitudinally elongated, about 30–60 μm × 10–15 μm large, often with pointed ends. Anticlinal walls are straight, smooth, and 1 μm thick and the periclinal walls are flat and smooth. Stomata are about 50 per mm^2, of average size 40 μm × 30 μm, and possessed superficial guard cells. No ligule pit cuticles could be prepared.

Comparison. Kidston (1893*a*, p. 80; 1911, p. 151) suggested that *L. macrolepidotus* was a larger form of *L. laricinus* and Crookall (1964, p. 310) doubtfully united the two. All the described specimens of *L. macrolepidotus* seem to be of large slabs of bark presumably coming from the main trunk or large branches; but while accepting that there were possibly smaller branches bearing smaller leaf cushions it is not yet proven that these were necessarily of the *L. laricinus* kind. *L. macrolepidotus* has leaf cushions which are more flattened than those of *L. laricinus* and they possess ligule pit apertures which are more distinct and relatively more separated from the leaf scars. The epidermal cells are about the same size in the two species but the anticlinal walls are thicker in *L. laricinus* (2 μm) than in *L. macrolepidotus* (1 μm). *L. laricinus* has 250 stomata per mm^2 with guard cells in pits (6–10 μm deep) but *L. macrolepidotus* has less stomata (50 per mm^2) and superficial guard cells.

The 'young branches' figured by Renault (1882, fig. 4) are excluded from this species in agreement with Kidston (1893*b*) and Crookall (1964). They seem to be more like *L. acerosus* or to a very similar species. The specimen described by Kidston (1893*b*) from the lower Carboniferous of Scotland is also excluded and described here as the holotype of *L. grangeri* sp. nov.

Lepidophloios grangeri sp. nov.

Plate 36, figs. 1–4; text-fig. 6

1893*b* (?) *Lepidophloios macrolepidotus* Goldenberg; Kidston, p. 560.
1964 *Lepidophloios laricinus* Sternberg; Crookall, pars, p. 310, pl. 74, fig. 6 (inverted).

Material. Holotype, K 1828 from above the Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire—within the Limestone Coal group of the Carboniferous Limestone Series of the Namurian (D_3 Coral brachiopod Zone and E_1 age of the goniatite notation, according to Macgregor in Trueman 1954).

The type specimen, which is the only known one referable to this species, is a 100 mm broad slab of compressed bark on an ironstone nodule. Cuticle was easily obtained from the exposed upper cushion surfaces but could not be prepared from the overlapped underlying lower surfaces. The ligule pit cuticles were unfortunately very cracked and only small fragments were therefore obtained.

Diagnosis. Exposed portions of leaf cushions broader than long. Ligule pit apertures adjacent to upper angles of leaf scars. Cushion surface smooth with no keel. Epidermal cells from central area of cushion longitudinally elongated, about 60–70 μm $\times$ 15 μm large. Epidermal cells from sides of cushion roughly isodiametric, 15–20 μm large. Anticlinal walls straight, smooth, 1 μm thick. Periclinal walls flat, smooth. Stomata about 150 per mm^2 over the whole cushion surface; average size 40 $\times$ 25 μm. Guard cells level with epidermal surface. Ligule pit about 230 μm broad; lining cells rectangular, longitudinally elongated, about 45–55 μm $\times$ 12 μm large.

Derivation of name. From the type locality.

EXPLANATION OF PLATE 36

Figs. 1–4. *Lepidophloios grangeri* sp. nov. 1, K 1828 from above the Craw Coal, No. 4 Mine, Grange, Boness, Linlithgowshire, $\times$2. 2, 3, cushion cuticle, slide no. PF 2900. 2, $\times$200; 3, $\times$600. 4, ligule pit cuticle; slide no. PF 2898, $\times$100.

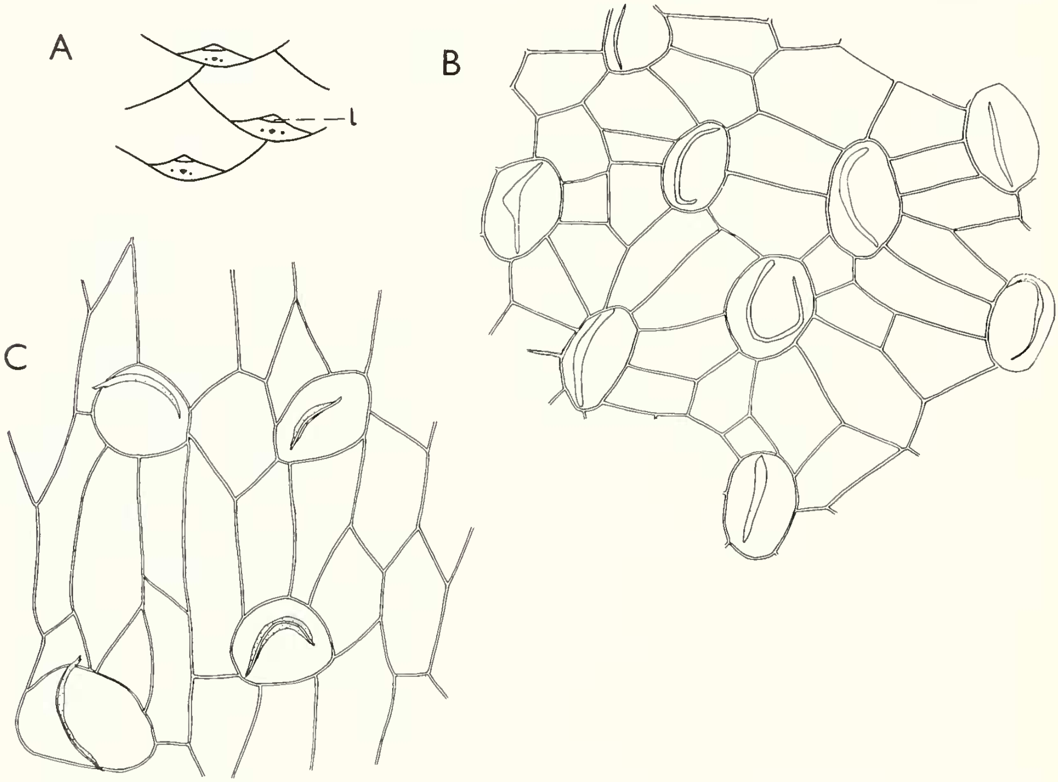
Figs. 5–7. *Lepidophloios acadianus* Dawson from Joggin Mine, Nova Scotia, Canada, 5, K 2318, $\times$0·5. 6, K 2323, $\times$1. 7, cushion cuticle from K 2323; slide no. PF 3131, $\times$200.

THOMAS, *Lepidophloios*

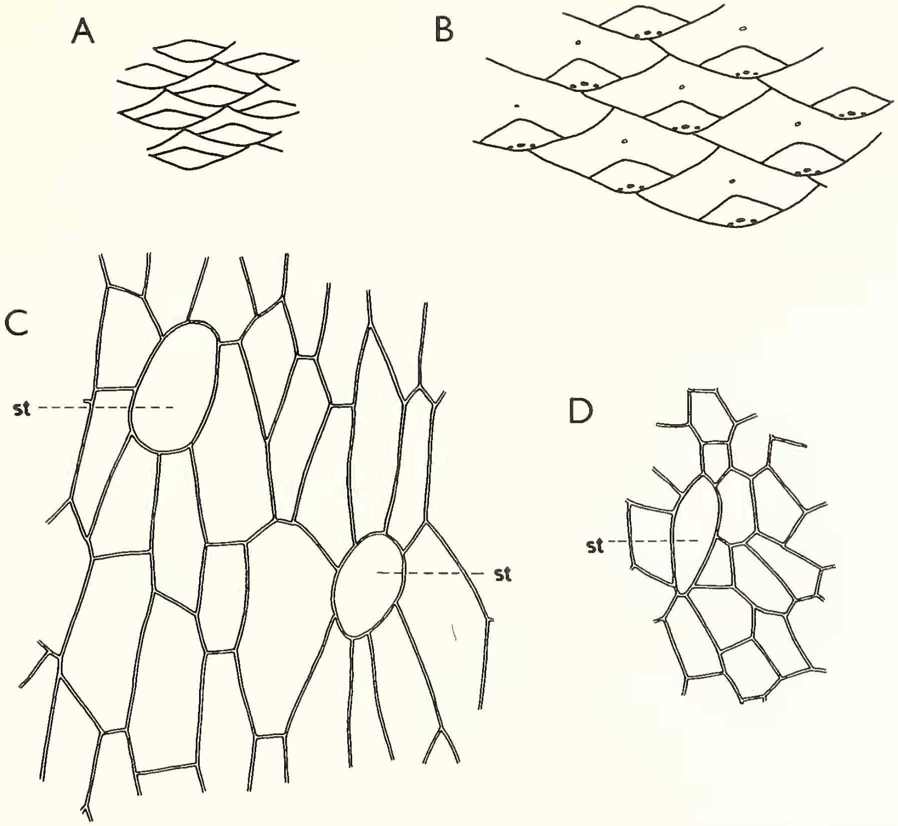
Comparison. The type specimen has been included within *L. macrolepidotus* and *L. laricinus*, but it can be distinguished from both of these species on cushion morphology and cuticle characters. The ligule pit aperture is adjacent to the leaf scar in *L. grangeri* but is clearly separated from the scar in the other two species. The epidermis has elongated cells in the central area and isodiametric cells on the lateral portions so it is similar to that of *L. laricinus*, but different to that of *L. macrolepidotus* which has only elongated cells. *L. laricinus* differs in having shorter cells in the central region even though the cells from the lateral areas are of comparable size to those in *L. grangeri*.

The stomata are of comparable size in all three species, but their frequencies differ. They are 150 per mm^2 in *L. grangeri*, 50 per mm^2 in *L. macrolepidotus*, and 250 per mm^2 in *L. laricinus*. The guard cells are also sunken in pits in *L. laricinus* whereas in the other two they are superficial.

L. grangeri also differs from the other species of *Lepidophloios* described here in coming from the Lower and not from the Upper Carboniferous. The other Lower Carboniferous species, *L. scoticus* Kidston, has been shown to possess a variety of leaf cushion sizes and shapes, but none is really like those of *L. grangeri*. The largest



TEXT-FIG. 6. *Lepidophloios grangeri* sp. nov. K 1828. A, leaf cushions, $\times$ 1. l—ligule pit aperture. B, C, cushion cuticle, $\times$400; drawn from the undersurface. B, cuticle from the non-median areas; slide no. PF 2900. C, cuticle from the median areas; slide no. PF 2899.



TEXT-FIG. 7. *Lepidophloios acadianus* Dawson. A, K 2324, × 1. B, K 2323, × 1. C, D, cushion cuticle from No. 2323, ×400, st—stomata. C, cuticle from the median area of the cushion; slide no. PF 3131. D, cuticle from the non-median area of the cushions; slide no. PF 3132.

cushions of *L. scoticus* have exposed areas which are longer than broad in contrast to those of *L. grangeri*. The lower edges of the leaf scars are also much flatter and the ligule pit apertures are separated from the leaf scars. No cushion cuticles have yet been described from *L. scoticus* so no comparison can be made of epidermal features, but even without this additional information the two types of cushion appear sufficiently different for species distinction.

Lepidophloios acadianus Dawson

Plate 36, figs. 5–7; text-fig. 7

1866 *Lepidophloios acadianus* Dawson, pp. 163, 168, pl. 10, fig. 45.
1868 *Lepidophloios acadianus* Dawson, p. 489; text-fig. 171.
1888 *Lepidophloios acadianus* Dawson, p. 166; text-fig. 44.

Material. K. 2318–2324 from Joggin, Canada.

All seven specimens were identified by Dawson as *L. acadianus* and K 2324 is labelled as 'fragment of type'. The exposed areas of the downturned cushions are all broader than long, with the leaf scars at their extreme bases except in K 2318 where a small portion of the cushion can be seen below the scars. Cushion surfaces are flat with no keels and the ligule pit apertures are clearly separated from the leaf scars.

Cuticle description. The epidermis is the same from the cushion surfaces above and below the leaf scars. The epidermal cells on the central areas of the cushions are elongated longitudinally and are 40–70 μm $\times$ 18–30 μm large, while the cells on the cushion are roughly isodiametric and about 15 μm large. Stomata are about 130 per mm^2 and of average size 45 μm $\times$ 33 μm. The guard cells are usually level with the epidermis but are occasionally sunken in 3 μm deep pits.

Comparison. Dawson published three identical accounts of this species but figured the leaf cushions upside down and without ligule pits. He believed *L. acadianus* to be closely allied to *Ulodendron majus* Lindley and Hutton and *L. laricinus* Sternberg; while Kidston (1901, p. 158), Bell (1944, p. 93), and Crookall (1964, p. 311) believed it to be conspecific with *L. laricinus*. *U. majus* is a completely different type of stem which possess permanently attached leaves and not downwardly directed leaf cushions (Thomas 1967*b*) so it has little in common with this species. *L. laricinus* is naturally similar, but can be distinguished by both cushion morphology and cuticle characters. The exposed parts of the cushions are relatively narrower with more rounded lower angles, the foliar prints are relatively higher on the leaf scars and the ligule pits are more distinct. *L. laricinus* also has larger epidermal cells, more stomata than *L. acadianus*, and the guard cells are normally sunken in pits.

DISCUSSION

Lepidophloios, like the other genera of arborescent lycopods, has been interpreted differently by various authors. Confusion and differences of opinion have existed over the range of species variation and over the very number of species which were thought to exist. Previous workers have used just leaf cushion morphology to identify their specimens, but recent work on other genera (Thomas 1967*a*, *b*, 1970) has shown how epidermal characters are clearly of immense value for this purpose. Therefore epidermal cell sizes and shapes, stomatal sizes, numbers, and distributions were studied in a range of species to see if they were similarly useful in this genus.

L. laricinus and *L. acerosus* are the two commonest species which are relatively easily distinguished on a combination of cushion characters, but at times they have been thought to be conspecific and have been also linked with other species of *Lepidophloios* and even *Lepidodendron*. Clearly the differences in cushion morphology can be thought to be insufficient for species distinction so there is some divergence of opinion here. However, if one takes the two 'recognizable forms' and looks at their epidermal details there are additional characters available for comparison. In this instance, such extra information clearly points to a continued separation of the two species. Similar epidermal evidence indicate that *Lepidophloios macrolepidotus*, *L. grangeri*, and *L. acadianus* are recognizable as distinct species and can not be thought of as growth forms of *L. laricinus* as has been often suggested.

Epidermal studies are thus once again of great value and the information gained has helped to crystallize a better idea of the various species. It has hopefully provided a sounder basis for understanding the range of species variation and for identifying new material.

The other important aspect of this type of study is that it should allow us to recognize growth forms of the various species. Previous work by Walton (1935), Andrews and Murdy (1958), and Eggert (1961) has suggested that Lepidodendralean trees grew by dichotomizing apices which progressively diminished in size. Therefore shoot diameter is no indication of age for the smaller shoots were merely more terminal and were not young shoots which had not yet enlarged by large amounts of secondary thickening, i.e. large shoots were formed from large apices while small shoots were formed from small apices. Some secondary thickening did occur but only in a manner which seems to have accentuated the primary growth form, for apparently the trunk and main branches were thickened much more than the smaller terminal shoots. Leaf growth also varied proportionally to shoot diameter, so in both *Lepidodendron* and *Lepidophloios* the narrower branches have smaller leaf cushions while only the very terminal shoots seemed to retain the distal foliage parts of their leaves. There are, however, certain major differences which existed between these two genera regarding the effects of limited secondary growth on the leaf cushions. Shoot expansion in *Lepidodendron* apparently did not initially affect the actual leaf cushions, but separated them instead by a gradual growth of the intercushion areas (Thomas 1966). In *Lepidophloios*, however, the situation appears to be rather different for the leaf cushions apparently never separated as in *Lepidodendron*. Those specimens suggesting such a separation (e.g. *Lepidophloios macrolepidotus*) have now been shown to be rather different with the intercushion areas being really narrow strips of shale protruding from between the overlapping leaf cushions. Instead of separating, the cushions appear to have enlarged and bulged further outwards and downwards. Indeed, the specimens of *L. acerosus* discussed above indicate that the cushions were originally of the *Lepidodendron* type. Then by expansion they would have bulged outwards and downwards synchronously with the enlargement of the shoot. Obviously much more evidence is needed to clarify our ideas of this particular method of growth and it would be much better if such stages could be demonstrated in species other than *Lepidophloios acerosus*. Unfortunately we are dealing with growth stages and this is always a major problem, because it is the growing points which are the least likely to become fossilized.

The other point of interest which centres around such a peculiar type of shoot growth is the usefulness of cushion enlargement to the growing plant. The question of photosynthetic efficiency of the arborescent lycopods has been broached several times but not in direct relationship to *Lepidophloios*. Andrews and Murdy (1958) and Andrews (1961) thought these plants possessed relatively small amounts of photosynthetic tissue because only the smallest twigs retained their leaves. Then the demonstration of numerous stomata on the leaf cushions suggested that the stems were much more photosynthetic than previously thought (Thomas 1966). While Chaloner and Collinson (1975) have since shown that *Sigillaria* possessed even more stomata per unit area than *Lepidodendron* and suggested that the increased amount of potential photosynthetic activity might help to explain their ability to grow with only a crown of leaves. What we may see in *Lepidophloios* is a further attempt to increase the photosynthetic ability of these plants, for such an increase in cushion size would appear to result in the production of more photosynthetic tissue. Perhaps we could take this to be the very reason for leaf cushion enlargement and the evolutionary change from the *Lepidodendron* type of cushion.

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REFERENCES

ANDREWS, H. N. 1961. *Studies in Palaeobotany*. John Wiley and Sons, New York. 487 pp.

—— and MURDY, W. H. 1958. *Lepidophloios*—an ontogeny in arborescent lycopods. *Am. J. Bot.* **45**, 552–559.

ARBER, E. A. N. 1914. On the fossil floras of the Wyre Forest, with special reference to the geology of the coalfield and its relationships to the neighbouring Coal Measure areas. *Phil. Trans. R. Soc. Ser. B*, **204**, 365–445.

BELL, W. A. 1944. Carboniferous rocks and fossil floras of Northern Nova Scotia. *Mem. geol. Surv. Can.* **238**, 276 pp.

CHALONER, W. G. 1967. *In* BOUREAU, E. (ed.). *Traité de Paléobotanique*. II. Masson et Cie, Paris, 437–485.

—— and COLLINSON, M. E. 1975. Application of SEM to a sigillarian impression fossil. *Rev. Palaeobot. Palynol.* **20**, 85–101.

CROOKALL, R. 1929. *Coal Measure plants*. Edward Arnold, London. 77 pp.

—— 1939. The plant 'break' in the Carboniferous rocks of Great Britain. *Bull. geol. Surv. G.B.* **1**, 13–24.

—— 1964. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. G.B. Palaeontology*, **IV**, pt. 3, 217–354.

DAWSON, J. W. 1866. On the Conditions of the Decomposition of Coal, more especially as illustrated by the coal formation of Nova Scotia and New Brunswick. *Q. Jl geol. Soc. Lond.* **22**, 95–169.

—— 1868. *Acadian Geology*. 2nd edn. Oliver and Boyd, Edinburgh. 694 pp.

—— 1888. *Geological Survey of Plants*. D. Appleton and Co., New York. 290 pp.

EGGERT, D. A. 1961. Ontogeny of Carboniferous Arborescent Lycopsida. *Palaeontographica*, **108B**, 43–92.

ETTINGSHAUSEN, C. VON. 1854. Die Steinkohlenflora von Radnitz in Böhmem. *Abhandl. k.k. geol. Reichsant.* **I**(3), No. 3. Vienna. 74 pp.

FEISTMANTEL, O. 1875. Die Versteinerungen der Böhmischen Kohlenablagerungen. *Palaeontographica*, **23**, 175–236.

GOLDENBERG, F. 1855–1862. *Flora Saraepontana fossils—Die Pflanzenversteinerungen des Steinkohlengebirges von Saarbrücken*. **I** (1885), 38 pp.; **II** (1857), 60 pp.; **III** (1862), 47 pp.

JONGMANS, W. J. 1929. *Fossilium Catalogus* II, Plantae Pars 15, Lycopodiales II, 53–523. W. Junk, Berlin.

—— 1930. Ibid., Pars 16, Lycopiodes III, 329–650.

KIDSTON, R. 1886. *Catalogue of the Palaeozoic Plants in the Department of Geology and Palaeontology, British Museum* (*Natural History*). London. 288 pp.

—— 1893*a*. The Yorkshire Carboniferous Flora. *Trans. Yorks. Nat. Union*, **18**, 65–128.

—— 1893*b*. *Lepidophloios*, and on the British species of the Genus. *Trans. R. Soc. Edinb.* **37** (3), 529–563.

—— 1894. Fossil Flora of the South Wales Coal Field and the Relationship of its strata to the Somerset and Bristol Coal Field. Ibid., 565–614.

—— 1901. Carboniferous Lycopods and Sphenophylls. *Trans. nat. Hist. Soc. Glasg.* **6** (N.S.), 25–140.

—— 1902. Flora of the Carboniferous Period. *Proc. Yorks. geol. polytech. Soc.* **14**, 334–370.

—— 1911. Les vegetaux houillères recueillis dans le Hainaut Belge. *Mém. Mus. r. Hist. nat. Belg.* **4**, 282 pp.

—— 1917. The Forest of Wyre and the Titterstone Clee Hill Coal Fields. *Trans. R. Soc. Edinb.* **51**, 999–1084.

LINDLEY, J. and HUTTON, W. 1831–1837. *The Fossil Flora of Great Britain: or Figures and Descriptions of the Vegetable remains found in a Fossil State in this country.* 3 vols. London. **I** (1831–1833), pp. li+223; **II** (1834–1835), pp. 206; **III** (1836–1837), pp. 205.

NĚMEJC, F. 1934. Critical remarks on Sternberg's *Lepidodendron dichotomum. Bull. int. Acad. tchéque Sci.* 35 ann., 75–79.

—— 1946. Further critical remarks on Sternberg's *Lepidodendron dichotomum* and its relations to the cones of *Sporangiostrobus* Bode. Ibid. 47 ann. 35–43.

—— 1947. The Lepidodendraceae of the coal districts of central Bohemia (a preliminary study). *Acta Musei Nationalis Prague*, 3B, **2,** 45–87.

POTONIÉ, H. 1899. *Lehrbuch der Pflanzenpalaeontologie.* Ferd, Dümmlers Verlagsbuchhandlung, Berlin. 402 pp.

REMY, W. and REMY, R. 1959. *Pflanzenfossilien.* Akademie Verlag, Berlin. 285 pp.

RENAULT, B. 1882. *Cours de botanique fossile.* G. Masson, Paris. 194 pp.

SCHIMPER, W. P. 1870. *Traité de Paleontologie Végétale, ou la Flore du Monde primitif dans ses reports avec les formations geologiques et la Flore du Monde actuel.* Vol. 2. J. Baillière et Fils, Paris. 522 pp.

SEWARD, A. C. 1890. Notes on *Lomatophloios macrolepidotus* (Goldg.). *Proc. Camb. phil. Soc.* **7** (2), 43–47.

STERNBERG, C. VON. 1820–1838. *Versuch einer geognotisch-botanischen.* Darstellung der Flora der Vorwelt. Leipzig and Prague. Pt. 1 (1820), 24 pp.; pt. 2 (1821), 33 pp.; pt. 3 (1823), 39 pp.; pt. 4 (1824), 42 pp.; pts. 5 and 6 (1833), 80 pp.; pts. 7 and 8 (1838), 291 pp.

STOCKMANS, F. and WILLIÈRE, V. 1953. Vegetaux Namuriens de la Belgique. *Assoc. Étude Paléont. Stratigraph. Houillères*, Publ. 13, Brussels. 382 pp.

THOMAS, B. A. 1966. The cuticle of the Lepidodendroid stem. *New Phytol.* **65,** 296–303.

—— 1967*a*. The cuticle of two species of *Bothrodendron* (Lycopsida; Lepidodendrales). *J. nat. Hist.* **1,** 53–60.

—— 1967*b*. *Ulodendron* Lindley and Hutton and its Cuticle. *Ann. Bot.* N.S. **31,** 775–782.

—— 1970. Epidermal studies in the interpretation of *Lepidodendron* species. *Palaeontology*, **13,** 145–173.

—— 1974. The Lepidodendroid stoma. Ibid. **17,** 525–539.

WALTON, J. 1935. Scottish Lower Carboniferous Plants: The Fossil Hollow Trees of Arran and their Branches. *Trans. R. Soc. Edinb.* **58,** 313–337.

WEISS, C. E. 1871. Fossile Flora jüngsten Steinkohlen-formation und des Rothliegenden im Saar-Rhein Gebiete. *K. Akad. d. Wissench. Berlin*, Teil 2, Heft 2, 141–212.

ZALESSKY, M. D. 1904. Végétaux fossiles du terrain carbonifère du Donetz, I, Lycopodiales. *Trudȳ geol. Kom.* N.S. **13,** 126 pp.

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